Safe for saplings; safe for seeds?

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Abstract

In wood pastures spatial associations of tree saplings with nurse structures such as unpalatable plants are generally explained as associational resistance; *i.e*. reduced herbivory by association with a defended neighbour. However, these associations may result from other underlying processes that occur at the seed stage. Here we tested whether the observed associations between *Picea abies* tree saplings and nurse structures could also be explained by higher soil seed densities under versus outside nurse shrubs, or by reduced seed removal inside versus outside nurse structures. Further we tested for differential effects of the main seed predator groups on seed removal and establishment, both in gaps and in dense vegetation.

We sampled in total 640 soil cores from inside and outside canopies of eight *Crataegus monogyna* shrubs and compared densities of *P. abies* seeds. Seed removal was studied inside and outside the canopies of four different nurse structures: *C. monogyna*, *Gentiana lutea*, rocks and tree stumps. The effects of cattle, birds, rodents and insects on seed removal and seedling establishment were studied using selective exclosures both in gaps and in dense vegetation.

Soil seed densities under and outside shrubs did not differ significantly. Seed removal was considerable (85%), indicating the importance of seed removal as limiting factor for tree regeneration in wood pastures. In contrast to our expectations, seed removal was significantly higher under all four nurse structures then outside. The subsequent exclusion of cattle, birds and rodents reduced seed removal and increased establishment, but the individual contribution of each of these groups was relatively small, while the contribution of insects was greater. Seed removal was higher and, consequently, seedling establishment lower in dense vegetation than in the gaps.

Our findings show that the earlier observed spatial associations between tree saplings and unpalatable plants, rocks and tree stumps are unlikely to be caused by an initially higher soil seed density or by reduced seed removal under these structures. Those structures were reported earlier to enhance tree sapling survival by offering protection against cattle grazing, but they appear not to protect tree seeds. This study shows the complexity of tree establishment in wood pasture ecosystems: apparently, safe sites for tree saplings are not safe for seeds.

Keywords: *Picea abies*; Seed predation; Safe sites; Nurse effects; Facilitation; Wood pastures; Seedling establishment

1. Introduction

Spatial association of tree saplings and nurse plants is a commonly observed phenomenon in a wide range of ecosystems. Proposed mechanisms leading to such associations are numerous: nurse plants may for instance reduce soil temperature, alter the water- or nutrient content of the soil or provide shelter from high irradiance or from extreme low or high air temperatures (e.g. Rousset and Lepart, 1999). In grazed environments observed spatial associations between tree saplings and unpalatable plants (avoided by herbivores because of mechanical or chemical defence mechanisms) are mostly attributed to associational resistance, *i.e*. reduced herbivore damage due to a defended neighbour (Bakker et al., 2004; Kuiters and Slim, 2003; Milchunas and Noy-Meir, 2002; Olff et al., 1999; Rebollo et al., 2002; Rousset and Lepart, 2000; Rousset and Lepart, 2002). However, little is known about the relative importance of such protection against herbivory for explaining these observed associations. Nurse plants may additionally favour the arrival of wind- or animal dispersed seeds (seed trapping) (de Viana et al., 2001), reduce the level of seed predation (e.g. birds prefer foraging in open habitat where they can escape from predators (Kelt et al., 2004), but see Castro et al. (1999), Hulme and Borelli (1999) and Vander Wall (1994) for contrasting preferred foraging by rodents under protective structures), or improve conditions for seed

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germination. These alternative nurse effects may also contribute to the observed higher densities of tree saplings near nurse structures. Only few studies have tried to disentangle these different processes (e.g. Weltzin and McPherson, 1999) and we are not aware of any such study in grazed environments.

The wood pastures of the Swiss Jura Mountains (1000–1500 m a.s.l.) have resulted from hundreds of years of extensive agricultural activity, probably since the early middle ages, which transformed the closed forest into a semi-open landscape with isolated or small groups of trees in grazed grasslands. During the past 50 years these biologically rich and diverse systems have disappeared rapidly, mainly due to intensification or abandonment of land use (Gillet and Gallandat, 1996; Pywell et al., 2002), and they are presently highly endangered. Little is known about the dynamics of wood pastures. Such information is a requirement for sustainable management of this ecosystem. In preceding studies on tree regeneration in Swiss wood pastures we found spatial associations between saplings of *Picea abies* and unpalatable plants, rocks and tree stumps (Smit et al., 2005), and we showed that unpalatable plants facilitate the survival of nearby planted tree saplings via associational resistance (Smit et al., 2006). Our aim in this study was to test whether additional mechanisms, already active at the seed stage, could contribute to the observed spatial associations between nurse structures and tree saplings. In three sub-studies we examined: (1) natural soil seed densities under and outside nurse shrubs; (2) seed removal under and outside nurse structures; (3) effects of cattle, birds, rodents and insects on seed removal and seedling establishment using selective exclosures. We hypothesised that (1) we would find higher soil seed densities under nurse shrubs; (2) we would find lower seed removal under nurse structures; (3) the subsequent exclusion of cattle, birds and rodents would lead to a reduction in seed removal and to an increase in seedling establishment.

2. Methods

2.1. Study species

2.1.1. P. abies (L.)

Karsten is the dominant tree species in the wood pastures of the Swiss Jura Mountains. It is an evergreen and shade-tolerant species reaching an age of 200–400 years. The seeds are wind dispersed and are released on warm and dry days in late autumn and winter, but are sometimes retained until spring (Schmidt-Vogt, 1987). Secondary dispersal on snow by wind (especially of high altitude species that are winter dispersing) could move seeds up to several hundred meters (Greene and Johnson, 1996). Commonly reported post-dispersal seed predators of conifers in Central and Northern Europe are birds (Fringilla spp.), rodents (*Apodemus sylvaticus* L., *Clethrionomys glareolus* Schreber and *Microtus agrestis* L. (Schreiner et al., 2000)) and insects, such as ground beetles (Carabidae) and lygaeid bugs (Lygaeidae) (Nilson, 2000; Nystrand and Granstrom, 2000).

2.2. Study sites

Our study sites are located in the central part of the Swiss Jura Mountains, with a mean annual temperature of 3–5 °C, annual precipitation of 1400–2000 mm and Jurassic limestone as the principal soil parent material. The first study site is situated at 1150–1260 m a.s.l. in the Communal de La Sagne (6°47′N, 47°3′E). This wood pasture of ca. 400 ha is freely grazed by both cows (369) and horses (15) every year between mid-May and the end of September. The second study site at la Petite Ronde is situated at 1126 m a.s.l (6°28′N, 46°53′E) and is grazed by cows from mid May till September according to a rotation system. Our selected enclosure measured 8.2 ha and was grazed for four rotational periods (each ca. 14 days) by a herd of 24 heifers. We selected these two study sites for the presence of structures (rocks, shrubs, tree stumps or patches of unpalatable plants) and associated tree saplings, needed for testing our hypotheses. The estimated density of these structures is ca. 50 per ha and *P. abies* is the dominating tree species in and around both study sites.

2.3. Study 1: soil seed densities

In March 2004, after main seed release, we compared soil seed densities under and outside the canopies of eight *Crataegus monogyna* shrubs of comparable sizes (mean height: 122 cm; mean diameter: 103 cm) in site 1. Here *P. abies* saplings are spatially associated with unpalatable plants, among which *C. monogyna* (Smit et al., 2005), and higher soil seed densities under the shrubs could explain these observed associations. The randomly selected shrubs were widely spaced over the study site, not being directly situated under a mature *P. abies* tree. At each shrub we put four 50 cm × 50 cm plots under- and four plots outside the shrub canopy (at 1.5 m from the edge of the crown's projection), one at each cardinal orientation. In each plot we took 10 soil cores with a gardeners' bulb planter (5 cm diameter, 3 cm deep) according to a systematic grid pattern, leading to a total of 640 soil cores. We stored these soil samples at 4 °C until further analysis. Then the soil cores were put in a water container (extended sink/float test) and sieved through a mesh in order to retrieve and count all *P. abies* seeds (Van Delft et al., 1997; de Viana et al., 2001). Data were analysed using a paired *t*-test: soil seed densities under the canopy of the *Crataegus* shrubs (pooled over the four orientations) were compared with the controls outside the shrub canopy. We used the pooled data as seed densities did not vary significantly between orientations.

2.4. Study 2: seed removal

Before the arrival of cattle (28th–29th of May 2004) we conducted an experiment in site 1 using four different nurse structure types: the shrub *C. monogyna*, the unpalatable herb *Gentiana lutea*, rocky outcrops and tree stumps. We compared the removal of experimentally sown seeds under the structures with their corresponding controls at 1.5 m distance. Of each structure type we randomly choose 30 replicates equally

distributed over the study area, hence we selected a total of 120 structures. Per structure we established eight 10 cm × 10 cm sub-plots: four under and four outside the structure canopy, one at each cardinal orientation. Sub-plots were marked with small wooden sticks of 0.5 cm × 5 cm pushed in the soil with only 1 cm visible. We considered this marking method adequate for not affecting removal rates. In early May 2004 we sowed 50 cold-stratified *P. abies* seeds per sub-plot; seeds were obtained from a local seed supplier. Our selected seed density was relatively high (5000 seeds/m^2), but corresponds to natural seed load of *P. abies* (up to 3500 seeds/m^2) documented in other studies (Nilson, 2000). Under optimal conditions 94% of the stratified *P. abies* seeds germinate between 10 and −14 days after sowing (personal communication seed supplier). After 2 weeks we revisited the plots and counted the number of missing seeds, damaged seeds (with holes or split in two), germinated seeds and the remaining intact seeds. Additionally we recorded the vegetation cover in each sub-plot (structure cover excluded) using a continuous scale from bare soil (0) to dense vegetation (9). Four out of the 120 originally selected structures were destroyed by human activities, so we present data of the remaining 46,400 sown seeds. Seed data were analysed with a generalised linear model (normal distribution, log-link function) with vegetation cover as a continuous predictor and structure and position (inside–outside structure) as categorical predictors. We defined seed removal rate as the sum of damaged and missing seeds divided by the originally sown 50 seeds per sub-plot. As response variable we used the seed removal rates averaged across sub-plots (the four orientations). Extremely low germination rates, probably due to high removal rates, occurred in all treatments and did not warrant further statistical analysis.

2.5. Study 3: selective exclosures

We conducted an experiment in both sites using selective exclosures to identify the effects of the main potential post-dispersal seed predator groups (birds, rodents and insects) of *P. abies*. Furthermore, we included vegetation cover as a factor in this experiment, using natural gaps (an area of ca. 20 cm × 20 cm without any vegetation, resulting from trampling cattle) and dense vegetation (high cover of grasses and herbs in grassland). In mid July 2004 we sowed 128 plots (10 cm diameter circles) with 50 cold-stratified seeds in either natural gaps or dense vegetation, all regularly distributed over an area of ca. 500 m^2. Then, we applied one of the four following treatments (Fig. 1): 'CBRI': no exclosure, open to cattle (C), birds (B), rodents (R) and insects (I); 'BRI': cow exclusion, but open to birds, rodents and insects: a small metal 10 cm × 10 cm × 25 cm exclosure; 'RI': cow and bird exclusion, open to rodents and insects: an exclosure as 'BRI' with a metallic 1 cm^2 mesh, raised 5 cm from the soil; and 'I': exclusion of cattle, birds and rodents, but open to insects: as in 'RI' but with the mesh touching the soil. In principle all four treatments were also open to slugs but, as no slugs were observed during this study, we considered their effects unimportant here. Differences in seed removal between the four treatments allowed us to identify the effects of each seed predator group. Each of the four treatments was replicated eight times in open and dense vegetation at both sites, resulting in 128 plots, based on a full factorial design for the factors site, treatment and vegetation type (assuming additive and not interactive effects of the seed predator groups).

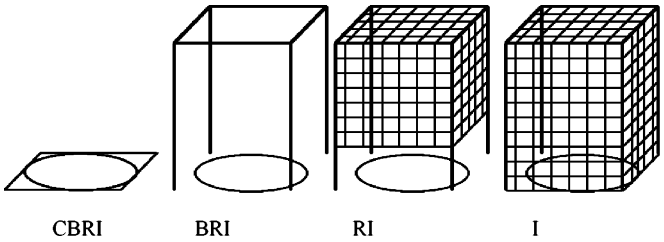

Fig. 1. Treatments applied in the seed removal experiment. CBRI: open to cattle (C), birds (B), rodents (R), and insects (I); BRI: cow exclusion, open to birds, rodents and insects; RI: cow and bird exclusion, open to rodents and insects; I: cow, bird and rodent exclusion, open to insects. Each 10 cm circle contained 50 stratified seeds of *P. abies*.

Five and 12 weeks after sowing we intensively searched and counted the number of damaged (split in half or with holes), germinated (aerial parts visible) and intact seeds in each plot. Germinated seeds still alive 12 weeks after sowing were recorded as established. We also searched for seeds and seedlings that were washed out or displaced into the direct surroundings of the plots (ca. 5 cm). Removal rates may be exaggerated by background losses due to wind, rain or activity of soil invertebrates, but comparison between treatments still provides a relative measure of the effects of the different seed predator groups. We acknowledge that seed removal is only an indication for, and not an accurate measure of, seed predation. Data were analysed with repeated measurements ANOVA. We used seed removal after 5 and 12 weeks and establishment as dependant variables and site (2), treatment (4) and vegetation type (2) as categorical predictors. Differences between levels of significant predictors were tested with Tukey HSD tests.

3. Results

3.1. Study 1: soil seed densities

We found a mean soil seed density of 5.48 seeds in the 10 soil cores per 50 cm × 50 cm plot, equivalent to 279 seeds per m^2. Soil seed densities under and outside shrubs, 5.66 ± 3.01 and 5.31 ± 2.68 (means ± S.D.), did not differ significantly (Paired *t*-test: d.f. = 7, *t*-ratio = − 1.376, $P = 0.211$). Thus, this study does not support the hypothesis of increased soil seed density under nurse shrubs.

3.2. Study 2: seed removal

Two weeks after sowing, the majority of the seeds (85.0%) were missing, 3.4% were damaged and only 0.14% of the 46,400 initially sown seeds had germinated (11.1% were left untouched). Seed removal (missing + damaged) was significantly affected by position (under or outside), but not by

Table 1
Results of generalised linear model (normal distribution, log-link function) on the effects of vegetation cover, structure type (tree stump, rock, shrub or *G. lutea*) and position (inside or outside structure canopy) on seed removal 2 weeks after sowing

Source of variation	d.f.	Log-likelihood	χ^2	*P*-values
Vegetation cover	1	332.265	0.3619	0.547
Structure type	3	329.455	5.9828	0.112
Position	1	316.845	31.2015	<0.001
Structure type × position	3	330.803	3.2868	0.349

Data is averaged over the four sub-samples (orientation) per position of each structure.

structure type and vegetation cover (Table 1). In contrast with our expectations seed removal was higher inside structure canopies than outside (0.88 ± 0.05 and 0.82 ± 0.06, respectively, means ± S.D.), irrespective of the type of structure (no significant structure by position interaction term).

3.3. Study 3: selective exclosures

Twelve weeks after sowing, 79.7% of all sown seeds were removed, 17.3% had germinated, only 1.0% was found damaged and 2.0% was still intact. Repeated measures ANOVA on the three response variables (seed removal after 5 and 12 weeks and establishment) showed overall significant effects of site, treatment and vegetation, and no significant interactions between factors (Table 2D). The final seed removal rate was higher in site 1 than in site 2 (0.77 ± 0.02 and 0.80 ± 0.02, respectively). Furthermore, seed removal was higher in dense vegetation (0.83 ± 0.02) than in gaps (0.76 ± 0.02), and seedling establishment was lower in dense vegetation (0.148 ± 0.02) than in gaps (0.215 ± 0.02) (Table 2B and C, respectively). The treatment effects showed a consistent pattern: stepwise exclusion of seed predator groups resulted in a gradual decrease in seed removal and increased final seedling establishment (Fig. 2). After 5 weeks seed removal was significantly higher in 'CBRI' than in 'I', and after 12 weeks higher in 'CBRI' than in 'RI' and 'I' (Tukey HSD tests, Fig. 2). Correspondingly, seedling establishment was significantly lower in 'CBRI' than in the three exclosure treatments, which in addition indicates large effects of cattle on final seedling establishment.

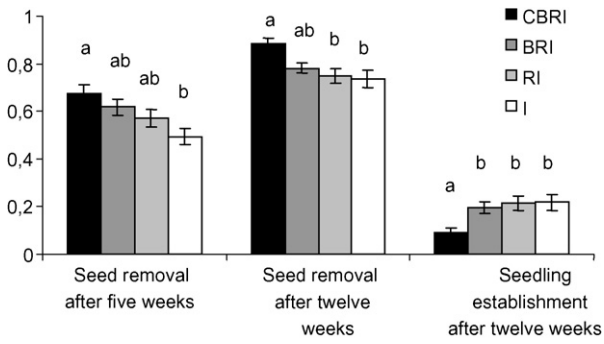

Fig. 2. Mean (±S.E.) seedling establishment and seed removal rate 5 and 12 weeks after sowing, for all four treatments. Black bars: open to all animal groups (CBRI); dark grey bars: cow exclusion (BRI); light grey bars: cow and bird exclusion (RI); white bars: cow, bird and rodent exclusion (I). Different letters indicate significant differences at alpha = 0.05 (Tukey HSD test).

4. Discussion

4.1. Study 1: soil seed densities

The soil seed densities of *P. abies* under and outside canopies of the shrub *C. monogyna* did not differ significantly in this study. Therefore, it is unlikely that the observed spatial associations between tree saplings and nurse structures are caused by higher seed densities under nurse structures. Such differences between densities of wind dispersed seeds under and outside nurse plants were found for other species in arid ecosystems, suggesting seed trapping (e.g. Flores and Jurado, 2003; Franks, 2003; Withgott, 2000). However, the findings of our study may be different for years with high seed production (mast years). Our observed seed density (279 seeds per m^2) was relatively low compared to the potential natural seed load of *P. abies* reported from closed forests (up to 3500 seeds per m^2) (Nilson, 2000). Chances on finding higher seed densities under nurse plants may well increase with an overall higher seed

Table 2
Univariate (A–C) and multivariate (D) results of repeated measures ANOVA on the three dependent variables establishment and removal of *P. abies* seeds after 5 and 12 weeks

Source of variation	d.f.	(A) Seed removal after 5 weeks		(B) Seed removal after 12 weeks		(C) Seedling establishment after 12 weeks		(D) Overall effects			
		MS	*F*	MS	*F*	MS	*F*	Wilk's value	*F*	Effect d.f.	Error d.f.
Site (S)	1	0.103	3.371	0.009	0.382	0.0004	0.018	0.889	4.11^{**}	3	99
Treatment (T)	3	0.169	5.532^{**}	0.118	5.068^{**}	0.1096	5.569^{**}	0.713	3.99^{***}	9	241
Vegetation (V)	1	0.096	3.133	0.148	6.356^{*}	0.1292	6.565^{*}	0.750	10.99^{***}	3	99
S × T	3	0.069	2.281	0.027	1.178	0.0238	1.212	0.860	1.71	9	241
T × V	3	0.016	0.518	0.053	2.267	0.0597	3.036	0.949	1.74	3	99
S × V	1	0.025	0.829	0.021	0.921	0.0134	0.679	0.933	0.78	9	241
S × T × V	3	0.027	0.774	0.034	1.480	0.0338	1.720	0.897	1.22	9	241

Explanatory variables: site (la Sagne or La Petite Ronde), treatment (CBRI, BRI, RI or I, see text), vegetation type (gaps and dense) and all interactions. Significant levels: $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

input. In order to test this hypothesis a comparative study on seed trapping effects during mast years and normal years is required. Another explanation for the observed relatively low seed density may be seed predation during the winter months. Birds (mostly *Fringilla coelebs*) were occasionally observed foraging on the hard snow surface in spring (C. Smit, personal observations). Given the constant accumulation of fresh snow during autumn and winter, predation of seeds from the surface is less probable, but can not be excluded.

4.2. Study 2: seed removal

Two weeks after sowing, the seed removal rate was relatively high (85%). Similar high removal rates of conifer seeds were found by others (e.g. Castro et al., 1999; Nystrand and Granstrom, 2000; Vander Wall, 1994), indicating the importance of seed removal as a limiting factor for tree regeneration in various ecosystems. So far, the magnitude of seed removal was to our knowledge never estimated for wood pasture ecosystems.

In contrast to our expectations seed removal was significantly higher under nurse structures than outside, irrespective of the type of structure. These results suggest that in our studied wood pastures tree stumps, rocks, shrubs and tall herbaceous plants do not prevent but rather enhance seed removal. This may be explained by the different foraging behaviours of the various granivorous groups (Kelt et al., 2004). In contrast to a number of bird species, rodents are reported to prefer foraging under 'safe' structures rather than in exposed habitat where they are more susceptible to natural enemies (Castro et al., 1999; Hulme and Borelli, 1999; Vander Wall, 1994). Granivorous insects may also prefer structure canopies, possibly for the shaded and humid conditions in this microenvironment.

Vegetation cover had no significant effects on seed removal. However, effects of vegetation cover were possibly confounded with the effects of the structures in this study. We isolated the effects of vegetation cover on seed removal in our third study and this topic is further discussed in the following section.

Given the results of this second sub-study, the earlier reported spatial associations between tree saplings and nurse structures are not likely to be caused by reduced seed removal under nurse structures.

4.3. Study 3: selective exclosures

Stepwise elimination of the main seed predator groups by selective exclosures decreased the removal of *P. abies* seeds and, consequently, increased the final establishment of seedlings. The differences in seed removal between each subsequent exclusion step were small: e.g. the non-significant differences between 'RI' and 'I' or 'BRI' and 'RI' (Fig. 2) indicate only modest effects of rodents and birds. At the same time, the significant difference between 'CBRI' and 'I' reflect the aggregated effects of cattle, birds and rodents. Hence, all seed predator groups seem to contribute to the seed removal, but the relative contribution of each group is little. Unfortunately, the experimental design does not allow testing interactions among cattle, rodents, birds and insects. Although potentially caused by an unknown factor, the relative contribution of insects ('I') seems the largest, with 49% and 74% seed removal 5 and 12 weeks after sowing, respectively. Nystrand and Granstrom (2000) reported a similar importance of insects, most notably ground beetles (Carabideae), as main post-dispersal seed predators of *Pinus sylvestris* in boreal forests. Similar to our results, the authors also found that small mammals and birds had only small effects on seed removal. It is unlikely that the *Picea* seeds used in our study were not attractive to rodents, as Schreiner et al. (2000) found significant seed removal by *A. sylvaticus*, *C. glareolus* and *M. agrestis* in mountain forests of south-western Germany. However, their study was performed in closed canopy habitat (*Abies alba–P. abies* stands), where densities of these rodents are expected to be higher than in our open wood pasture habitat. Moreover, the most commonly observed rodent in our site, *Arvicola terrestris*, is not granivorous but herbivorous. We acknowledge that determination of the presence of granivorous species in our sites only happened irregularly via visual observations for birds and via live traps for rodents, placed ca. 1 km from our study site to avoid influencing the experiment. A more systematic approach for all species groups over the entire course of the season (April–November) could facilitate the clarification of our findings. Seed predators responsible for seed removal in early spring in study 1 (e.g. birds) may not be the same as seed predators in summer in study 2 and 3 (e.g. insects). Similarly, the abundance of the main seed predator groups may vary between study sites, which could explain the significant site effect in the repeated measures ANOVA. For an accurate estimation of the actual seed predation a predator free and weather resistant control treatment would be required. Now, we attribute the observed removal of seeds largely to seed predators, but removal due to wind or soil invertebrates, although estimated as negligible, cannot be excluded.

The exclusion of cattle had only small and statistically not significant effects on seed removal, given the similarity between 'BRI' and 'CBRI'. However, excluding cattle led to a significant increase of seedling establishment. Cattle grazing may have reduced the number of established seedlings as these are usually completely uprooted when encountered (Smit et al., 2006). Further, trampling may have killed established seedlings or pressed seeds deeply in the soil causing death (Hulme and Borelli, 1999). So, despite high seed removal rates under structures, these findings could again indicate the importance of structures protecting established seedlings from cattle.

In dense vegetation seed removal was higher, and seedling establishment was lower, than in gaps (Table 2). Nystrand and Granstrom (1997, 2000) similarly found increased seed removal in dense vegetation and attributed this to granivorous insects, which prefer the shaded and more humid conditions. Their findings coincide well with the relatively high seed removal we found in our 'I' treatments, which similarly suggest high importance of insects as seed predators. Interestingly, it appears that a dense vegetation cover has similar effects on seed removal as the selected protective structures of study 2 (tree

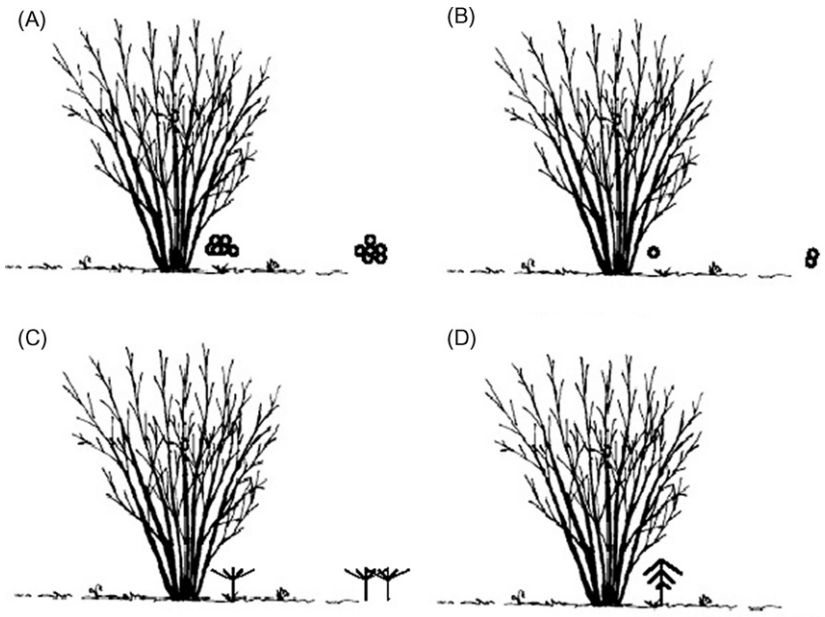

Fig. 3. Schematic overview of suggested effects of nurse structures (here depicted as a shrub) on the survival of *P. abies* from seed to sapling: (A) equivalent seed densities arrive under and outside structures; (B) seed removal is higher under structures than outside; (C) this results in reduced seedling establishment under structures; (D) only under structures are established seedlings protected against cattle, leading to increased sapling survival under structures.

stumps, rocks, shrubs, unpalatable plants). Apparently, it is the presence of a protective cover (being dense vegetation or a shrub, tree stump, etc.) that increases the chance on seed removal. In study 2, no significant effects of vegetation cover on seed removal were found; possibly because the effects of structure and vegetation cover could not be disentangled with the applied experimental design.

An additional explanation for lower seedling establishment in dense vegetation (besides increased seed removal and effects of cattle) is increased root competition. Root competition is reported to prevent establishment of trees in grasslands (Jurena and Archer, 2003) and is expected to play an important role in our studied wood pastures; the continuous grazing has created regular dense patches with grasses, which are difficult to penetrate by tree seedlings.

Seed removal in study 2 was already 85% after 2 weeks, whereas this was 'only' 80% after 12 weeks in study 3. A few factors may be responsible for this observed difference. First of all, study 3 started mid July which is 1 month later than study 2. Within this month some important environmental factors changed in the field: cattle started grazing at the start of study 3 (cattle were absent during study 2) and the vegetation changed considerably (height, density, dominance of species, etc.). These factors probably indirectly affected abundance, type and activity of the seed predators, resulting in lower seed removal rates over time.

4.4. Synthesis

We have shown that (1) soil seed densities under and outside nurse shrubs were not different; (2) seed removal was higher under than outside nurse structures; (3) stepwise exclusion of cattle, birds and rodents reduced seed removal rates. We conclude that the earlier reported spatial associations between tree saplings and nurse structures (Smit et al., 2005, 2006) are not likely to be caused by seed trapping or by protective effects of the nurse structures against seed predators. Unpalatable plants may protect established tree saplings against cattle browsing and enhance seedling survival (Smit et al., 2006), but they do not successfully protect seeds from predators. It seems that safe sites for tree regeneration are different for the various life stages of *P. abies*: the best places for seedlings to survive appear not to be the best places for seeds to germinate and establish. Similar differences in suitability of sites for seeds and seedlings, also known as spatial discordance, have been reported for a wide range of woody species, predominantly for animal dispersed (fleshy) fruits (e.g. Garcia and Ortiz-Pulido, 2004; Jordann o and Herrera, 1995; Traveset et al., 2003), but see Houle (1998) for an example of wind dispersed *Betula alleghaniensis*. A schematic overview of the effects of structures during the early life stages of *P. abies* is depicted in Fig. 3. Our findings indicate the complexity of tree regeneration in wood pasture ecosystems and that, for a complete understanding, all life stages should be taken into account. This complicates the fine-scale modelling of population and community dynamics and makes sustainable management of wood pastures more difficult. In order to maintain natural regeneration of trees in wood pastures, a requirement for the long-term existence of this system, focus of the management should be on preserving the heterogeneity in the landscape with abundant protective structures. In contrast with an intensive grazing regime, a suitable extensive grazing regime would allow the establishment and maintenance of shrubs and unpalatable plants. Despite considerable seed loss under and outside these structures, they do provide shelter at the seedling and sapling phase against cattle, which will eventually lead to

the formation of few isolated trees in the landscape. By this, such structures significantly contribute to the maintenance of the unique pasture woodland ecosystem.

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